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Behavioral Responses of Crustacean Larvae to Rates of Temperature Change

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Abstract. The ontogeny of behavioral responses of larvae of the crabs *Rhithropanopeus harrisii* and *Neopanope sayi* to rates of change in temperature were analyzed using a video system. A temperature decrease evoked an ascent in both species. The threshold rates of decrease for Stages I and IV zoeae of *R. harrisii*, and Stage I zoeae of *N. sayi*, were 0.06, 0.1, and 0.09°C min^{-1}, respectively. Stage IV zoeae of *N. sayi* were unresponsive to any rate of decrease. Larvae descended upon a temperature increase. For Stages I and IV zoeae of *R. harrisii* and Stage I of *N. sayi* the threshold rates of temperature increase were 0.07, 0.24, and 0.18°C min^{-1}, respectively. Stage IV zoeae of *N. sayi* were again unresponsive. In general, there was an ontogenetic change in responsiveness as Stage IV zoeae of both species were less sensitive than Stage I zoeae. The average absolute amounts of temperature change needed to evoke a response was independent of the rate of change at rates above threshold and ranged from 0.29 to 0.49°C for both species. A consideration of larval sinking rates and ascent speeds, as well as normal environmental temperature gradients, shows that larvae of both species can respond to the rates and amounts of temperature change found in their environments. These responses constitute a negative feedback system that could be used to regulate depth relative to temperature.

Introduction

Temperature change produces measurable alterations in the directional responses to light (phototaxis) and gravity (geotaxis), and the activity of crustacean larvae (for general reviews see Thorson, 1964; Forward, 1976; Sulkin, 1984). In phototactic studies, only narrow beams of light have been used as a stimulus source, rather than a light field that simulates the underwater angular light distribution. For *Callinectes sapidus*, larval phototaxis was not affected by temperature changes of 10°C (Sulkin and Van Heukelem, 1982). The only clear effect on *Rhithropanopeus harrisii* larvae was a slight increase in negative phototaxis by Stage I zoeae upon a temperature increase (Ott and Forward, 1976). Reductions in temperature within the range encountered by larvae did not alter phototaxis in any zoeal stage of *R. harrisii*. Nevertheless, there was a pronounced positive geotaxis by Stage IV zoeae of *R. harrisii* at high temperatures (30 and 35°C) and a sinking response by Stage I zoeae (Ott and Forward, 1976). Similarly, *C. sapidus* descended by passive sinking upon exposure to temperatures of 27.5°C or greater (McConnaughey and Sulkin, 1984).

Activity, as measured by linear swimming speed, has the pattern of an increase in speed with an increase in temperature (Sulkin *et al.*, 1980; Kelley *et al.*, 1982) up to a certain high temperature where inactivity (sinking) occurs (Welsh, 1932; Yule, 1984). In contrast, the swimming speed of Stage I zoeae of *C. sapidus* was not modified by a temperature decrease (Sulkin *et al.*, 1980).

Several studies suggested that responses to high temperatures did not result from sensitivity to a rate of temperature increase but rather to an absolute upper temperature (Ott and Forward, 1976; McConnaughey and Sulkin, 1984). Although the upper temperature may vary with species, this generalization was substantiated by measurements of behavioral responses in sharp thermoclines. If the upper temperature in the thermocline was above this limit, then larvae ascent stopped at the thermocline. Alternatively, larvae ascended through the thermocline if the upper temperature was below the absolute upper limit. Remarkably, 10°C thermoclines had

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no inhibitory effect on an ascent, which has led to the conclusion that, for many species, temperature gradients in nature will not prevent upward movements (Kelley *et al.*, 1982; Sulkin *et al.*, 1983; McConnaughey and Sulkin, 1984).

Considering these past studies, larval crustaceans seem relatively unresponsive to temperature changes. Nevertheless, the behavioral responses that do occur upon changes in temperature can be summarized. A temperature increase to temperatures at and above the absolute upper limit evokes negative phototaxis, positive geotaxis, and sinking, all of which lead to downward movement. An ascent does not occur upon a reduction in temperatures. Activity decreases with decreasing temperature and at extremely low temperatures larvae are totally inactive (*e.g.*, Ott and Forward, 1976).

A limitation of past studies is that larval behavior was studied at very sharp thermoclines and upon exposure to step changes in temperature. Sharp thermoclines can exist in nature, but most often larvae encounter a rate of change in temperature that depends upon the vertical gradient and rates of vertical movement. The present study was undertaken (1) to determine the lowest rates (threshold) of temperature change that evoke ascent and descent responses, (2) to measure the absolute amount of temperature change that must occur before larvae respond, and (3) to compare these rates and absolute amounts to those a larva could encounter in the water column. The study compares larvae of the crabs *Rhithropanopeus harrisii* and *Neopanope sayi* (family Xanthidae). These were selected because both live as adults in estuaries, but the behavior of *R. harrisii* larvae results in retention in upper estuarine areas (Cronin, 1982), whereas *N. sayi* larvae undergo development in lower estuarine and coastal areas (Sandifer, 1975; Dittel and Epifanio, 1982; Salmon *et al.*, 1986). Thus the larval species are taxonomically related, but they develop in different areas where they are potentially exposed to different temperature regimes.

Materials and Methods

Ovigerous specimens of *Rhithropanopeus harrisii* (Gould) were collected from the Neuse River estuary (North Carolina) from July to August 1989. Crabs were placed in 20 ppt seawater, which was passed through a 5-μm filter. Ovigerous *Neopanope sayi* (Smith) were collected from the Newport River estuary (North Carolina) from August to September 1989, and females were held in 32 ppt seawater, which was the approximate salinity at the collection site. Larvae of both species were reared at the same salinity in which the crabs were maintained at a temperature of 25°C. This acclimation temperature was chosen because it approximates the average summer temperatures where the larvae undergo development (Stefansson and Atkinson, 1967; Kirby-Smith and Barber, 1979).

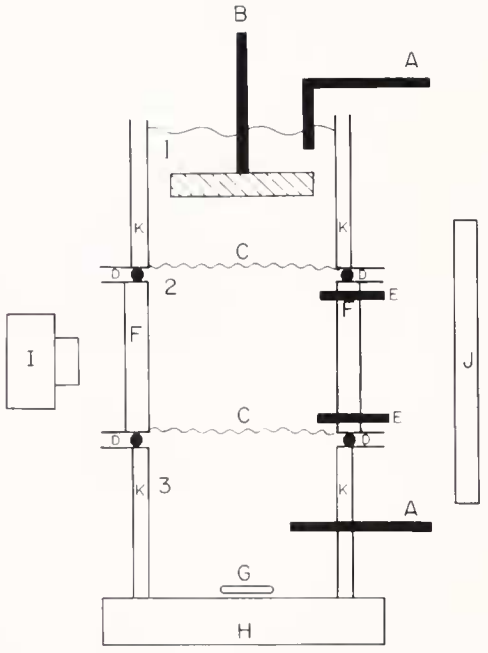

Figure 1. Horizontal view of test chamber consisting of equal size cylindrical upper (1), test (2), and lower (3) sections (not drawn to scale). A—insulated input/output Tygon tubes connected to peristaltic pump; B—stirring paddle connected to a variable speed stirring motor; C—75 μ mesh plankton netting; D—O-ring; E—thermister probe connected to meter with digital readout; F—square water-filled chamber surrounding the test chamber; G—magnetic stirring bar; H—magnetic stirrer; I—video camera; J—far-red illumination light; K—thermal insulation. The video camera and thermisters were oriented perpendicular to each other in the actual chamber.

Specimens were reared in a controlled environmental chamber (Sherer, Model CEL4-4) on a 14:10 LD cycle. Throughout development, larvae were transferred daily to clean seawater and fed newly hatched *Artemia* spp. nauplii. Experiments were conducted with Stages I and IV zoeae, to test for an ontogenetic change in responsiveness because each species has four zoeal stages. All experiments were performed in mid photophase to avoid complications due to biological rhythms in behavior. Larvae were light-adapted to room fluorescent light (intensity = about 1 W m^{-2}) prior to all experiments. In most cases a minimum of five groups of larvae, each from a separate female, were tested in each experimental situation.

Experimental approach

Larval responses to different rates of temperature change were measured in a chamber having three vertical cylindrical sections (section height = 2.5 cm; diameter = 2.5 cm; Fig. 1). For temperature increase, high temperature water (above 25°C) was added to the upper section

and mixed by a slowly rotating paddle. Larvae were confined to the middle section by plankton netting (75 μ mesh) at the upper and lower boundaries; their behavior was monitored and recorded with a closed circuit television system. For viewing, animals were illuminated with far-red light (maximum transmission 775 nm), to which larvae are not responsive (Forward and Cronin, 1979). The lower section was used for temperature decreases. Low temperature water (below 25°C) was added and mixed with a magnetic stirring bar. Preliminary measurements of larval swimming indicated that slow stirring in the upper and lower sections had no apparent effect on movement.

Test water was initially the same water as that used for rearing larvae. This water was pumped through a coil of Tygon tubing situated in a separate water bath (Forma Scientific, Model 2095) and then into the test chamber. The section of tube from the bath to the chamber was insulated with a foam wrap. To insure that there were constant amounts of water in all chamber sections and constant flow through the center section, the waters of different temperature were delivered to the appropriate end section by a variable speed peristaltic pump (Buchler Instruments), and water was extracted at the same rate from the other end section by the same pump. For example, to induce a temperature decrease, low temperature water was pumped into the lower section while water was removed from the upper section at the same rate. Dye studies indicated laminar flow of water through the netting into the center section. Also, the maintenance of constant water levels in all chambers prevented hydrostatic pressure changes during experimentation. This procedure was important because larvae of both species are very sensitive to pressure changes (Forward and Wellins, 1989; Forward *et al.*, 1989).

The rates of temperature change were varied through differences in temperature between the input and acclimation temperature water and pumping rate. In most experiments the temperature difference remained constant and pumping rate was varied. The actual temperatures in the upper and lower subsections of the larval section of the test chamber were measured with two thermister probes (YSI; Model 423; Time constant 1.45 s) connected to separate digital meters (Omega Engineering, Inc.; Model 450-ATH; accuracy 0.1°C). The digital readouts from the probes were viewed by a second video camera and inserted in the video picture with a video screen splitter (Vision Industries, Inc.; Model U2705P). A record of time was also inserted into the picture by a Field/Frame Counter (QSI Systems, Inc.). In this way larval behavior, temperature, and time were recorded simultaneously on videotape. The actual rates of change in temperature were calculated from temperature measurements by the probe closest to the chamber section (upper or lower) where test seawater was added. Measurements by the lower probe were used for temperature decreases and upper probe for temperature increases. Specific rates of temperature change were determined directly from the experimental records. In each experiment the rate of temperature change quickly increased up to the maximum for each flow rate or temperature difference condition and then remained approximately uniform through the time when responses were measured.

Experimental procedures

The same general procedure tested for responses to temperature increases and decreases. Larvae were held in the rearing water in finger bowls (10.3 cm diameter) situated in a separate water bath that was maintained at the acclimation temperature (25°C). The room temperature was also kept at about 25°C. A group of approximately 75 Stage I or 25 Stage IV zoeae was placed in the test chamber in water from the maintenance finger bowl. Thus, the initial temperature in the test chamber was very close to 25°C. The peristaltic pump and videotape recorder were started after 1 min in darkness. Temperature changed at a specific rate and was first detected about 3 min after the pump was activated. The experiment continued until the temperature changed about 1.0°C. Larvae were then removed, the chamber rinsed with water at the acclimation temperature, and a new group of larvae placed in the chamber. The procedure was repeated. Larvae were only tested once at each rate of temperature change. If larvae were retested at a second rate on any particular day, the minimum time between testing was about 2.5 h. Larvae remained at 25°C in the water bath between tests, and there was no obvious change in behavior with multiple tests. To establish that the observed responses were not induced by water flow through the chamber, larvae were tested using the foregoing procedure at the maximum test flow rate with acclimation temperature water. In this way larvae experienced flow but no temperature change. This control also tested for changes in larval distributions over time due to random activity.

Analysis

All experiments were conducted with the test chamber illuminated only with far-red light. Because they were functionally in darkness in this situation, the possible behavioral responses to changes in temperature were changes in activity or geotaxis.

To analyze for behavioral responses, the test (larval) section of the test chamber was divided into three equal horizontal subsections by a template placed over the video screen. The number of larvae in each subsection was counted before (control) and after each 0.1°C

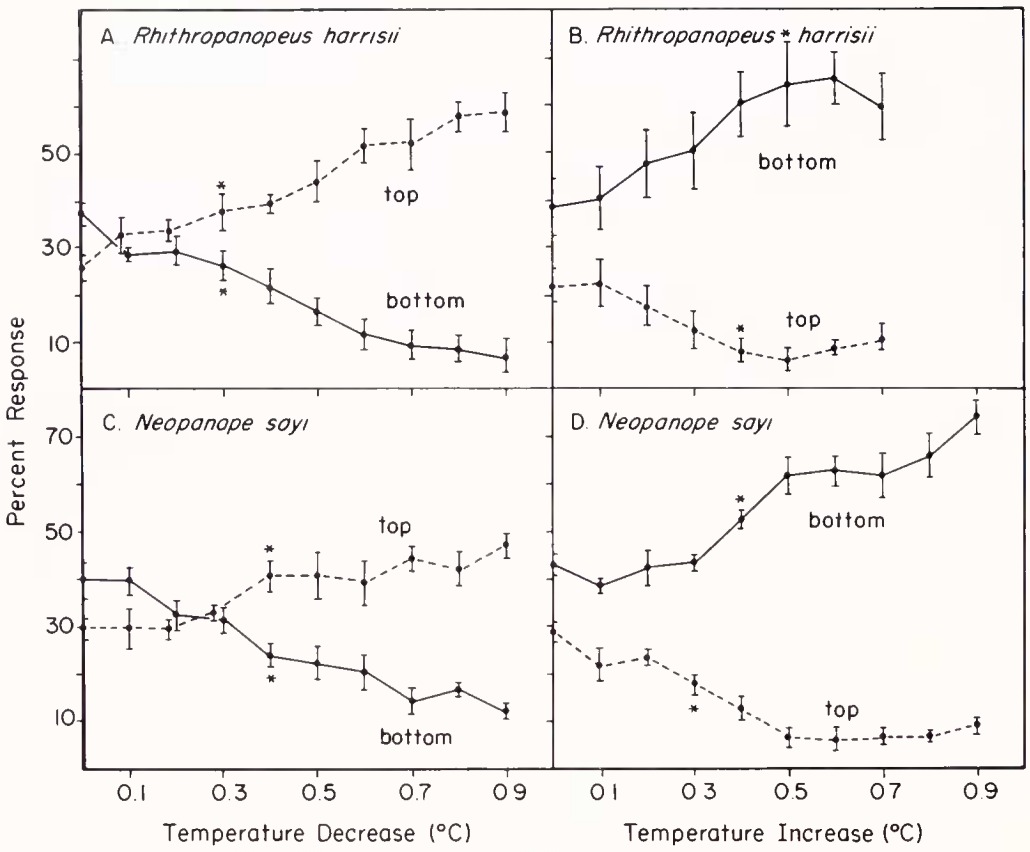

Figure 2. Percentage of Stage I zoeae of *Rhithropanopeus harrisii* (A, B) and *Neopanope sayi* (C, D) in the top (dashed line) and bottom (solid line) subsection of the larval section of the test chamber. Responses were measured after different absolute amounts of temperature change upon temperature decreases (A, C) and increases (B, D). These absolute temperatures are those in the bottom (A, C) and top (B, D) subsections of the test chamber. The rates of temperature change were 0.28 (A), 0.19 (B), 0.23 (C), and 0.28 (D)°C min^{-1}. Means and standard errors are plotted and the replicate sizes are 7 (A, B), 5 (C), and 6 (D). An asterisk indicates the lowest absolute temperature change to evoke a percent response that was significantly different ($P < 0.05$; Dunnett's t-test) from the control level, which is plotted at 0°C.

change. Control counts were made 30 s before the first 0.1°C change in temperature. The percentage of larvae in each subsection was calculated from these data. Response level was considered the percentage of larvae in the subsections after a 0.5°C change in temperature, because responses are clearly evident by this absolute amount of temperature change (Fig. 2).

Ascent and descent responses were expected upon a temperature decrease and increase, respectively. Thus the change in the percentage of larvae in the bottom subsection was monitored upon a temperature decrease, and, in the upper subsection, upon a temperature increase. Arcsine transformed data were used for statistical tests and to calculate means, standard deviations, and standard errors. Back transformed means and standard errors are plotted in the figures. If paired observations were made before (control) and upon stimulation (experimental) of each group of larvae, a t-test for paired comparisons was used to test for differences ($P < 0.05$). In cases where a control was compared to responses at different times after the beginning of stimulation, then the Dunnett's t-test for multiple comparisons with a control was used to test for significant differences ($P < 0.05$; Dunnett, 1964). A Z statistic testing differences between two proportions (Walpole, 1974) was used to test for differences between control and experimental distributions of individual trials.

Results

Response time course

The change in the percentage of larvae in the lower or upper subsections of the experimental chamber, upon an increase or decrease in temperature, respectively, is the response time course. Representative patterns are shown for Stage I zoeae at rates of temperature change that

evoked strong responses (Fig. 2). Initially the larvae were approximately evenly distributed in the test chamber, as the percentage of larvae in the top and bottom subsections was close to 33%. However, because the true values were not always 33%, the initial distribution was determined for each group of larvae, and the mean used as the control level for comparison with percentages upon a temperature change.

An ascent occurred upon a temperature decrease as indicated by a decrease in larvae in the bottom subsection and increase in the top subsection (Fig. 2A, C). For both *R. harrisii* (Fig. 2A) and *N. sayi* (Fig. 2C), significant changes co-occurred in the bottom and top subsections after a 0.3–0.4°C absolute temperature change. Thus, larvae leave the bottom subsection, and ascend to the top subsection, when the temperature decreases (Fig. 2A, C).

With a temperature increase, there was a descent; the percentage of larvae in the top subsection decreased, while it increased in the bottom subsection (Fig. 2B, D). For both species, the percentage of larvae changed significantly in the top subsection after a 0.3°C absolute temperature change, and after a 0.4°C change for larvae in the bottom subsection. This pattern (Fig. 2B, D) indicates that larvae left the top subsection and aggregated in the bottom subsection.

These response patterns were used to establish the analytical methods for the experiments. The percentage of larvae in the bottom subsection was monitored upon a temperature decrease. Because cooled water entered the test chamber at the bottom, larvae in the bottom subsection were initially exposed to the temperature decrease and responded first. Similarly, the percentage of larvae in the top subsection was monitored upon a temperature increase, because warmer water entered the test chamber from above. For both temperature decreases and increases, larval distributions were monitored before (control) and after a 0.5°C absolute change in temperature (experimental). The results shown in Figure 2 indicate that strong responses are evident by this amount of temperature change, and preliminary analysis showed that if larvae had not responded by the 0.5°C change, then they did not respond at greater absolute temperature changes.

Temperature decrease

Responses upon a temperature decrease were not due to fluid flow through the test chamber. Larvae were subjected to the maximum experimental flow rate, but not to a temperature decrease. Distributions were measured at the average time after the beginning of flow for the control and experimental measurements at this flow rate. The mean percentage of larvae in the bottom section never changed significantly with flow. This result also indicates random larval movements did not produce the observed responses.

In contrast, larvae ascended upon a temperature decrease. The lower rates of temperature decrease (threshold) to induce a response by Stages I and IV zoeae of *R. harrisii* (Fig. 3A, C) and Stage I zoeae of *N. sayi* (Fig. 3B) were 0.06, 0.1, and 0.09°C min^{-1}, respectively. A significant response was not displayed by Stage IV zoeae of *N. sayi* at rates up to 0.45°C min^{-1} (Fig. 3D). Thus, there was an ontogenetic change in sensitivity by both species, in which Stage I zoeae were more sensitive than Stage IV.

Temperature increase

Larvae descended upon an increase in temperature (Fig. 4). This response was not due to fluid flow or random movements. Using techniques for measuring responses to flow as described in the previous section, the mean percentage of larvae in the upper section did not change significantly between the control and experimental times (Fig. 4; plotted at rate 0° min^{-1}). The threshold rates for Stages I and IV zoeae of *R. harrisii* (Fig. 4A, C) and Stage I zoeae of *N. sayi* (Fig. 4B) were 0.07, 0.24, and 0.18°C min^{-1}, respectively. Stage IV zoeae of *N. sayi* were not responsive to any rate of temperature increase up to 0.35°C min^{-1} (Fig. 4D). These results indicate that, for both species, Stage I zoeae respond to slower rates of temperature increase than Stage IV zoeae.

Absolute temperature change

The absolute amounts of temperature change necessary to produce a significant response upon temperature decreases and increases were determined for each larval stage (Fig. 5). Determinations were made at those rates that produced a significant response (Figs. 3, 4). For each trial, the proportion of control larvae in the bottom (temperature decrease) or top (temperature increase) subsections was compared to the proportion of larvae after each 0.1°C change, until a significant difference was evident ($P < 0.05$; Z statistic for testing differences between two proportions). Mean absolute temperature values were then calculated for each rate (Fig. 5). Mean values did not vary significantly with rate of temperature change (one-way ANOVA) within each species, zoeal stage, and direction of temperature change. Thus an average value was calculated for a temperature increase and decrease at each zoeal stage (Table I). Mean values varied over a narrow range from 0.28°C to 0.49°C.

Discussion

The general responses of both test species of larvae were an ascent upon a temperature decrease and descent upon a temperature increase. Since all experiments were

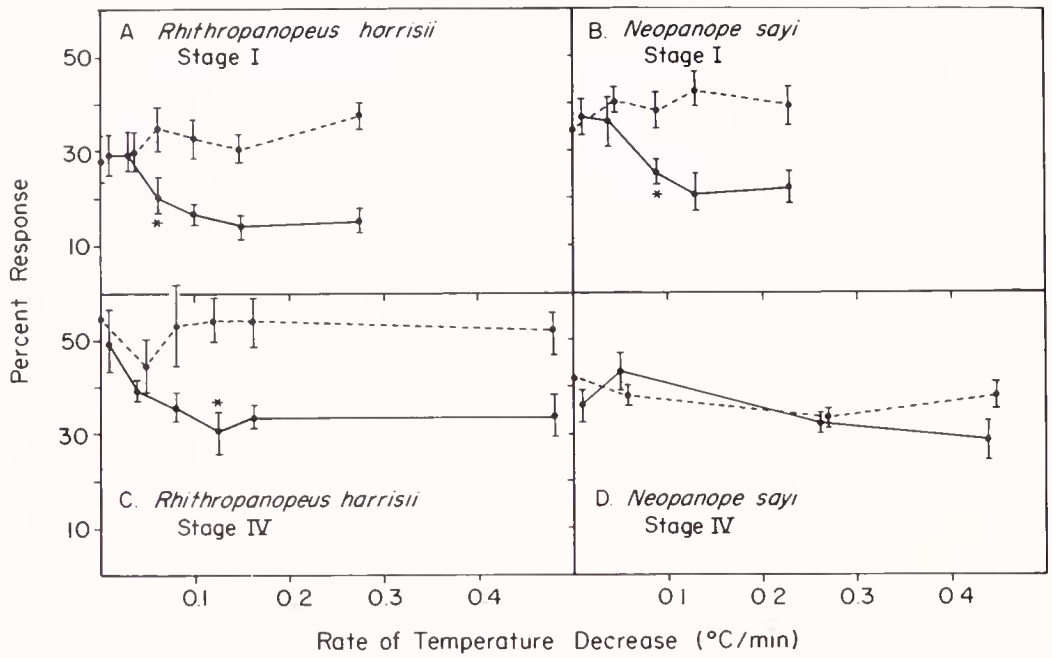

Figure 3. The percentage of Stages I and IV zoeae of *Rhithropanopeus harrisii* (A, C) and *Neopanope sayi* (B, D) in the bottom subsection of the test section before a temperature change (dashed line) and after 0.5°C absolute temperature change (solid line) at different rates of temperature decrease. The control for flow at the fastest test flow rate is plotted at 0°C min^{-1} rate of change. Means and standard errors are plotted and the average replicate size for A, B, C, and D was 6. Asterisks indicate the slowest rate of temperature decrease at which there is a significant difference between mean control and experimental percentages ($P < 0.05$; *t*-test for paired comparison.

conducted in darkness, the ascent could result from an activity increase or negative geotaxis, whereas the descent could involve sinking or positive geotaxis (Forward, 1988). The descent response upon a temperature increase has been observed frequently in past studies, in which larvae were exposed to step changes in temperature, but the ascent response at low temperatures is uncommon (*e.g.*, Ott and Forward, 1976). Because high temperatures usually occur in the upper part of the water column and low temperatures at depth, the behavioral responses of the two test species constitute a negative feedback system that could keep larvae at the acclimatization temperature.

For some crustacean species, such as *Callinectes sapidus*, there is a change in responsiveness to temperature throughout larval development (*e.g.*, Sulkin *et al.*, 1980). Sensitivity decreases with age for both test species. Stage I zoeae of *Rhithropanopeus harrisii* had lower threshold rates for temperature decrease (0.06°C min^{-1}) and increase (0.07°C min^{-1}) than Stage IV zoeae (decrease = 0.1°C min^{-1}; increase = 0.24°C min^{-1}). The ontogenetic change is greater for *Neopanope sayi*, because Stage I zoeae showed pronounced responses to temperature change but Stage IV zoeae were unresponsive to any test rate of temperature increase or decrease, which ranged up to 2.3–5.1 times greater than the threshold rates for Stage I zoeae (Figs. 3, 4).

To respond to a change in temperature, larvae must sense not only a rate of change in temperature but also a particular absolute amount of change. The necessary absolute amounts of temperature change varied slightly with rates of change (above threshold; Fig. 5) and during zoeal development. Average values ranged from 0.28 to 0.49°C (Table I). The fact that rates of change below threshold did not evoke a response (Figs. 3, 4) proves that both a sufficient rate of change and absolute amount of change must be present before a response occurs. At these subthreshold rates, the absolute amount of temperature change (0.5°C) was sufficient for a response, but larvae did not respond.

R. harrisii and *N. sayi* larvae respond at similar threshold rates and after similar absolute amounts of temperature change. An important consideration is whether this sensitivity is adequate for detection of vertical temperature gradients in their environment. Past laboratory studies of other species of crustacean larvae suggest that sharp thermoclines will not impede vertical movements because larvae pass through laboratory thermoclines that are greater than those in their natural environment. Nevertheless, temporary aggregations were observed at ther-

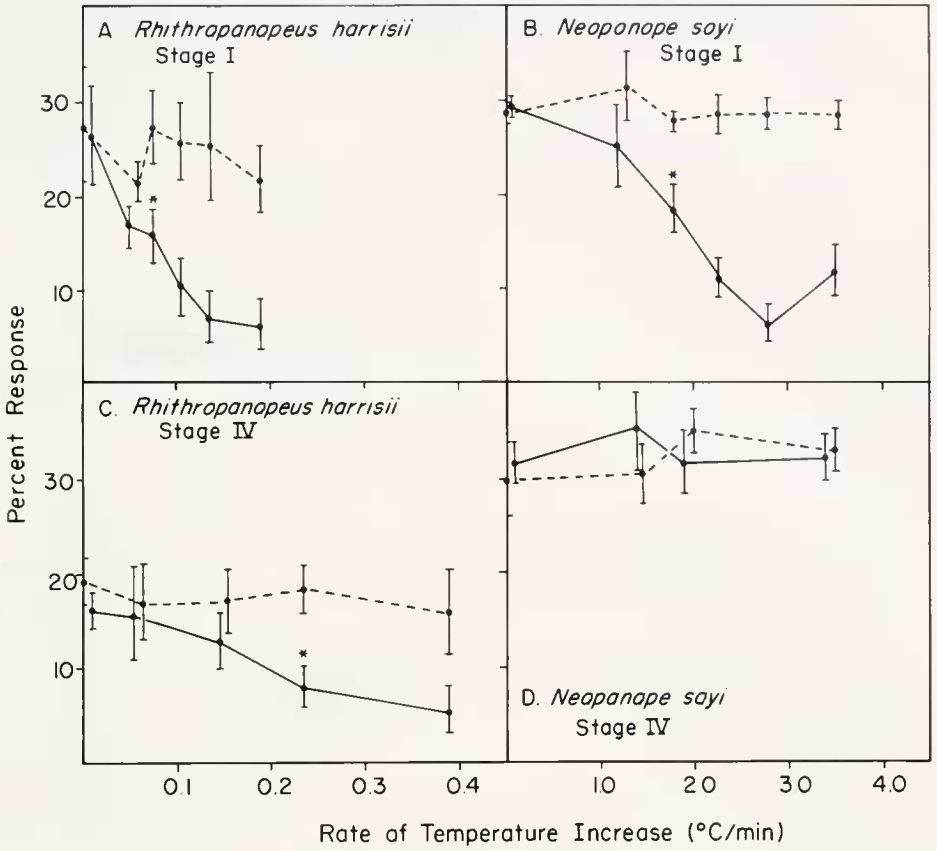

Figure 4. The percentage of Stages I and IV zoeae of *Rhithropanopeus harrisii* (A, C) and *Neopanope sayi* (B, D) in the top subsection of the test section before (dashed line) and after a 0.5°C absolute temperature increase (solid line) at different rates of temperature increase. The control for flow as measured at the fastest test flow rate is plotted at 0°C/min^{-1}. Means and standard errors are plotted. The average replicate size in A, B, C, and D are 6, 6, 7, and 7, respectively. Asterisks indicate the slowest rate of temperature increase at which there is a significant difference between control and test mean percentages ($P < 0.05$; *t*-test for paired comparisons).

moclines during vertical movements by *Eurypanopeus depressus* (Sulkin *et al.*, 1983) and *Callinectes sapidus* larvae (McConnaughey and Sulkin, 1984).

R. harrisii larvae are retained in upper estuarine areas (Cronin, 1982). Kirby-Smith and Barber (1979) measured environmental factors in an area (South River, North Carolina) close to the collection site for ovigerous *R. harrisii* where larvae consistently occur. Daytime temperature at the surface and bottom during the summer reproductive months of July and August (1974–1976) indicate that a temperature difference existed 80% of the measurement times. A conservative assumption is that temperature changed continuously from the surface to the bottom. Under these conditions, the average gradient was 0.9°C m^{-1}.

The threshold rates of detection by larvae and speeds of vertical movement were used to calculate the minimal gradient a larva could perceive. A conservative measure of speed of downward movement is larval sinking speed because larvae can also actively swim down. If *R. harrisii* sink continuously, then the minimal temperature decrease they can detect is 0.32°C m^{-1} for Stage I zoeae and 0.22°C m^{-1} for Stage IV zoeae (Table I). Using average ascent rates, the minimal increase in temperature they could detect is 0.19°C m^{-1} for Stage I zoeae and 0.63°C m^{-1} for Stage IV (Table I). Because these values are below the average gradient calculated from the measurements of Kirby-Smith and Barber (1979), *R. harrisii* larvae can detect changes in temperature in their environment.

N. sayi larvae inhabit low estuarine and coastal environments (Sandifer, 1975; Dittel and Epifanio, 1982; Salmon *et al.*, 1986). Pinschmidt (1963) measured surface and bottom temperatures in the Beaufort Inlet, which connects the Newport River estuary (where ovigerous *N. sayi* were collected) and the coastal waters. Measurements in July and August (1960–1961) indicate temperature differences were present 50% of the time.

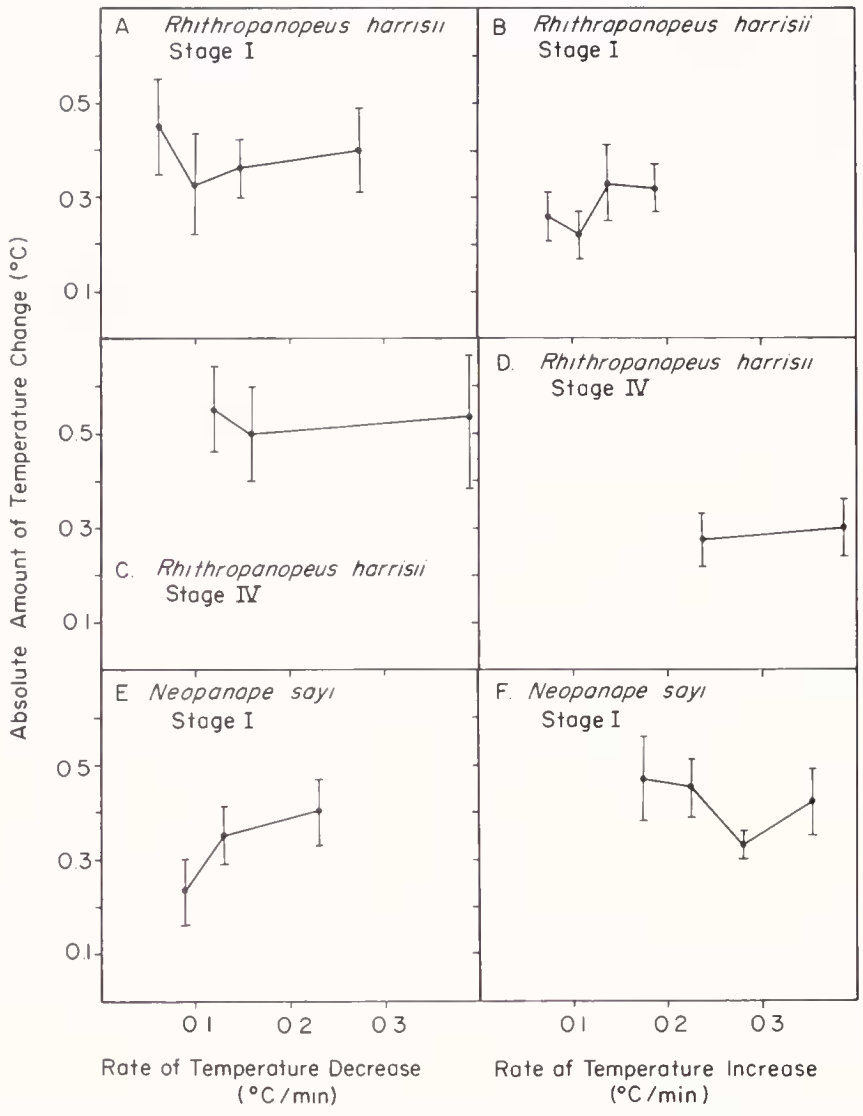

Figure 5. The amount of absolute change in temperature before a response to different rates of temperature decrease and increase by *Rhithropanopeus harrisii* (A, B, C, D) and *Neopanope sayi* (E, F) larvae. Means and standard errors are plotted. The average replicate size for all means was 5.

Again assuming a continuous change in temperature, the average gradient was 0.3°C m^{-1}. Stefansson and Atkinson (1967) extensively measured temperature in the coastal area seaward of the Beaufort Inlet at specific depth intervals. During the summer months, temperature was approximately equal in the upper 10 m, but at times differences approaching those measured by Pinschmidt (1963) were evident at deeper depths.

The gradients that can be perceived by *N. sayi* larvae were calculated using the same procedure as for *R. harrisii* larvae. The detectable gradient in temperature decrease for Stage I zoeae is 0.34°C m^{-1} and for a temperature increase is 0.94°C m^{-1} (Table I). Thus Stage I zoeae of *N. sayi* should be able to detect the average environmental gradients in temperature decrease, but require extreme gradients in temperature increase.

An additional consideration is the functional significance of responses to temperature change. Larvae of both species can respond to a temperature increase and decrease. The threshold rates are in the range of 0.1°C min^{-1} (2×10^{-3}°C s^{-1}), and the necessary absolute amounts of change are less than 0.5°C (Table I). Larvae do not respond to temperatures above some very high absolute upper limit as suggested by past studies (Ott and Forward, 1976; McConnaughey and Sulkin, 1984). These responses could be used to avoid extreme, adverse environmental temperatures. Since high temperatures usually occur near the surface and low temperatures oc-

Table I

Calculation of minimal detectable temperature change per m

Threshold rate temperature decrease ($°C\ s^{-1}$)	Mean sinking rate ($mm\ s^{-1}$)	Minimum detectable gradient of temperature decrease ($°C\ m^{-1}$)	Absolute amount of temperature decrease (°C)
Rhithropanopeus harrisii			
Stage I—1.0×10^{-3}	3.1	0.32	0.38
Stage IV—1.7×10^{-3}	7.8	0.22	0.49
Neopanope sayi			
Stage I—1.5×10^{-3}	4.4	0.34	0.34
Temperature increase	Mean ascent rate ($mm\ s^{-1}$)	Minimum detectable gradient of temperature increase ($°C\ m^{-1}$)	Absolute amount of temperature increase (°C)
R. harrisii			
State I—1.2×10^{-3}	6.3	0.19	0.28
Stage IV—3.9×10^{-3}	6.2	0.63	0.29
N. sayi			
Stage I—3.0×10^{-3}	3.2	0.94	0.41

Threshold rates are from Figures 3 and 4. Mean sinking (Latz and Forward, 1977) and ascent speeds (Forward and Wellins, 1989) for *R. harrisii* are at 20 ppt (rearing salinity), while those for *N. sayi* are at 32 ppt (Forward *et al.*, 1989). The minimum detection rate in $°C\ m^{-1}$ is calculated as (threshold rate/sinking-ascent rate)1000. The absolute amounts of temperature increase are mean values from Figure 5.

cur at depth, the ascent response upon a temperature decrease would move larvae upward out of cool water into warmer water. The opposite responses occur upon a temperature increase. Nevertheless, the high sensitivity of larvae to temperature change suggests that these responses may have an additional function than avoidance of extreme conditions. Temperature could be used as a cue to regulate depth at a particular optimum temperature or as a cue for depth maintenance in a particular water mass that has a characteristic temperature.

With the present study it is possible to evaluate the relationships of larval responses to environmental factors. For *R. harrisii,* responses to rate of change in light (Forward, 1985), hydrostatic pressure (Forward and Wellins, 1989), salinity (Forward, 1989), and temperature (this study) have been determined. Upon descending in a stratified water column, light intensity decreases, pressure increases, salinity increases, and temperature decreases. At rates of change that are within the range larvae can encounter while descending, each of the changes in these environmental factors induces negative geotaxis or an activity increase that results in an ascent.

In contrast, the opposite environmental changes upon an ascent produce weak responses, at best. *R. harrisii* larvae are unresponsive to rates of increase in light intensity (Forward, 1985) and rates of decrease in salinity (Forward, 1989) they are likely to encounter underwater. In darkness, a sinking response occurs upon a pressure decrease, but the threshold rate is much higher than that for a pressure increase (Forward and Wellins, 1989). Similarly, this study indicates larvae can respond to both increases and decreases in temperature, but the thresholds were always higher for responses to a temperature increase (Table I).

For *N. sayi,* responses to rates of changes in salinity (Forward, 1989), pressure (Forward *et al.,* 1989), and temperature (this study) have also been studied. Considering Stage I zoeae, a pronounced ascent is also induced by changes in these factors that are likely to occur upon descending in the water column. The opposite environmental changes produce weaker responses. *N. sayi* larvae are unresponsive to decreases in salinity (Forward, 1989). They respond both to pressures increases and decreases, but the threshold for a pressure increase was lower than that for a pressure decrease (Forward *et al.,* 1989). Finally, this study shows that larvae respond to temperature increases and decreases, but the threshold rate is higher for a temperature increase (Table I). Thus both *R. harrisii* and *N. sayi* larvae have asymmetrical responses to changes in environmental factors. These responses may keep larvae up in the water column and reduce the likelihood that they will encounter the bottom and its associated benthic predators.

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